



Original Research Article

Conversion of peat swamp forest to oil palm cultivation reduces the diversity and abundance of macrofungi

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ABSTRACT

Deforestation of tropical peat swamp forests is rapidly taking place across Southeast Asia to make way for agricultural expansion. Within forest ecosystems, macrofungi play a vital role, including wood decomposition and nutrient cycles. To reveal the effects of deforestation and land cover conversion on macrofungi in Southeast Asian tropical forests we assessed the relationship between environmental variables such as air temperature, relative air humidity, soil pH, soil moisture, canopy cover, canopy closure, habitat type (i.e., peat swamp forest, large-scale plantation, monoculture smallholding, and polyculture smallholding) and available substrata with macrofungal species richness and abundance. We sample macrofungi across four habitats on Peninsula Malaysia including peat swamp forest, large-scale plantations, monoculture smallholding and polyculture smallholding. We found that substrate richness had a positive effect on macrofungal morphospecies richness, while soil pH and air temperature had a negative effect. For macrofungal abundance, canopy closure and soil moisture had negative effects, whereas substrate richness and relative air humidity had positive effects. Our data showed considerable variation in functional group responses to environmental variables. The abundance of wood-inhabiting fungi was driven primarily by substrate richness, while relative air humidity, soil moisture, and habitat type play minor roles. The abundance of terricolous saprotrophic fungi was determined principally by habitat type, substrate richness, and relative air humidity. Macrofungal community structure was mainly influenced by substrate richness, followed by microclimates and soil characteristics. Our results can provide critical ecological data to support conservation stakeholders conserve macrofungi in natural and agricultural peatlands. Our study suggests that the expansion of oil palm monocultures, to the detriment of peat swamp forests, is likely to have negative effects on macrofungal biodiversity and further agricultural expansion should be prevented.

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1. Introduction

Fungi play a key role in the biosphere acting as decomposers and supporting nutrient cycling; consequently, they are considered to be effective biological indicators of soil health (Vasconcellos et al., 2016). There are approximately 5.1 million fungal species on Earth (Blackwell, 2011; Hawksworth, 2012), but 92% of them have not currently been described (Hawksworth and Luecking, 2017). More field research is required, especially in the tropics, to document macrofungal diversity using morphological and molecular identification (López-Quintero et al., 2012; Ambrosio et al., 2015; Iqbal et al., 2016). In forests, there are three main fungal functional groups that can be separated based on lifestyle and trophic status of species: ectomycorrhizal, wood-inhabiting, and terricolous saprotrophic fungi (Lin et al., 2005; Tedersoo et al., 2010). Saprobic fungi, the scope of our study, perform essential ecosystem functions decaying wood and decomposing litter and other organic substrata (Moore et al., 2004).

Macrofungi can be found in several types of habitats, including tropical peatlands (Shuhada et al., 2017). Despite their ecological importance, little is known about macrofungal communities in tropical peat swamp forests. Across Southeast Asia, peat swamp forests are being lost due to the conversion of forests to agricultural lands (Koh et al., 2011; Miettinen et al., 2012, 2016). Deforestation is one of the main causes of human-caused climate change, leading to increased temperatures and changing rainfall patterns at global and regional scales (Cramer et al., 2004; Li et al., 2018a; Malhi et al., 2008). Modifications in the macrofungal fruiting patterns caused by climate change have been reported from many regions (Gange et al., 2011; Kauserud et al., 2008; Yang et al., 2012). In addition, deforestation can cause changes in soil properties (Könönen et al., 2018), which influence the distribution of macrofungal species.

Only a few studies have focused on the relationship between macrofungal species composition and/or species richness and environmental variables including the richness of available substrata, especially in the tropics. Most of the existing studies have been conducted on ectomycorrhizal fungi (e.g., Yamashita et al., 2015; McGuire et al., 2015) and only a few on saprobic fungi (Borovička et al., 2010; Yamashita et al., 2015). A lot of the research on macrofungi has focused on well-known edible morphospecies such as *Pleurotus* sp. (Cogorni et al., 2014; Das et al., 2015). Casazza et al. (2017) reported that soil chemistry was the main driver of the occurrence and distribution of ectomycorrhizal and some saprobic fungi. While, Shuhada et al. (2017) found that thermophilic macrofungal *Schizophyllum* sp. are able to persist under less humid microclimates in oil palm plantations.

Up to now, no studies have been carried out comparing the most important environmental drivers of macrofungal species composition and species richness in peat swamp forest and oil palm plantations. Therefore, more targeted studies should have completed to describe more fungal species from the tropics and to reveal which of them are sensitive the most on human activities. The most influential environmental drivers of macrofungal species richness and species abundance should also be found in peat swamp forests.

The overall objective of this study was to assess and explain the potential environmental drivers of macrofungal species richness and species abundance in peatlands in Peninsular Malaysia to support conservation. Firstly, we assessed the relationship between macrofungal species richness and abundance and air temperature, relative air humidity, soil pH, soil moisture, canopy cover, canopy closure and substrate richness. Secondly, we assessed how different macrofungal functional groups respond to environmental variation. Thirdly, we examined the extent to which the environmental data is related to the macrofungal community structure. Lastly, we compared the substratum performance (the number, availability, and suitability of substrata for macrofungi) in logged peat swamp forests and oil palm plantations. This information would be highly valuable both for conservationists and industry stakeholders to understand the consequences of deforestation and to make sustainable land use plans for tropical peatlands.

2. Materials and methods

2.1. Study area

This study was conducted from December 2015 to January 2016 across four habitats consisting of: 1) peat swamp forest, 2) large-scale plantation, 3) monoculture smallholding and 4) polyculture smallholding (Fig. 1). The peat swamp forest is located in the North Selangor Peat Swamp Forest (NSPSF), with an area of 73,593 ha (N 3°40'26.56", E 101°4'29.52"), comprising three forest reserves: Sungai Karang Forest Reserve (50,106 ha), Raja Musa Forest Reserve (23,486 ha), and Sungai Dusun Wildlife Reserve (4330 ha). These peatland habitats include peat swamp forest and oil palm areas with different production systems and different vegetation structural characteristics (Azhar et al., 2017; Oon et al., 2019a; 2019b). The forest landscape is characterized by logged peat swamp forest species such as *Macaranga pruinosa*, *Campnosperma coriaceum*, *Shorea platycarpa* and *Ixora grandiflora*. Commercial logging at the NSPSF stopped 23 years ago. The original lowland dipterocarp forest covers only 5% of the whole area (Azhar et al., 2011, 2013).

The other three habitats are oil palm plantations with different management systems on former peat swamp forests. One of them is a large-scale oil palm plantation (>2000 ha) managed by a corporation. The other two oil palm plantation types are less mechanized smallholdings (<50 ha) managed by individual farmers. Two different management systems for smallholdings were surveyed in this study: monoculture and polyculture smallholdings. Similar to large-scale plantations, monoculture smallholdings are planted with oil palm exclusively. Polyculture smallholdings harbour oil palm plantations with other crops, such as banana (*Musa x paradisiaca*), cassava (*Manihot esculenta*), coconut (*Cocos nucifera*), breadfruit



Fig. 1. Peatland habitat types surveyed: natural peat swamp forest (top left), large-scale plantation (top right), monoculture smallholding (bottom left), and polyculture smallholding (bottom right).

(*Artocarpus altilis*), lemongrass (*Cymbopogon citratus*), mangoes (*Mangifera indica*), and pineapple (*Ananas comosus*). All the oil palm stands were approximately eight years old.

2.2. Sampling design and data collection

Within each habitat, a total of 60 circular plots of 20 m radius were established along a 500 m transect. Each transect started 50 m inside the border of each habitat. These plots were selected using a systematic sampling method with a random starting point according to Morrison et al. (2008). A geographical positioning device (GPS II Plus, Garmin Ltd., Olathe, Kansas) was used to record the geographical coordinates of each plot.

Following (López-Quintero et al., 2012), we visited each plot for 20–30 min after rainy days (at least 24 h after the rain stopped) to find macrofungal sporocarps. All plots were visited only once. Macrofungal sampling was conducted consistently across plots and habitats between 9.30 and 11.30 a.m. At each plot, all macrofungal species with at least one fruiting body were collected and identified to the genus level. A cluster was considered as one observation irrespective of the number of sporocarps in a cluster, following Brown et al. (2006) and Shuhada et al. (2017). We used research papers (e.g., Iqbal et al., 2016) and fungi websites (<http://www.indexfungorum.org>; <http://www.mycobank.org>) to identify fungal taxa and followed Kirk et al. (2008) for correct and current taxonomic names.

For each macrofungal sample we recorded the substrate where macrofungal sporocarps were found (Ye et al., 2019). We then calculated substrate richness for the whole plot based on the number of different substrate types on which sporocarps were present within a plot. The substratum types recorded were: branch (diameter > 2.5 cm), twigs (diameter < 2.5 cm), leaf litter, fruit shells (López-Quintero et al., 2012), living trees, trunks, soil (Gibbertoni et al., 2007), coarse wood, fallen tree, stump, oil palm frond, living oil palm, coconut trunk, and buttress.

At each plot, a series of environmental variables were measured. Air temperature and relative air humidity were measured using a mini environmental quality meter (Sper Scientific 850070, Sper Scientific Ltd., Scottsdale, United States) at 1 m height. Soil pH and soil moisture were recorded at a depth of 7 cm using a soil pH and moisture meter (DM-15, Takemura Electric Works Ltd. Tokyo, Japan). We measured the microclimate variables, soil pH, and soil moisture during solar noon (12.00 p.m.–2.00 p.m.) when the sun was directly overhead (Pereira et al., 2003). Three readings were subsequently taken at each plot and the average of the readings was recorded. At the center of each plot, at 0.5 m height, we measured canopy closure using a DSLR camera (DSC-HX-400V, Sony Corporation, Tokyo, Japan) and calculated canopy cover by applying the MATLAB software (Mathworks, Natick, Massachusetts, USA). Canopy cover was characterised by the percent forest area filled by the vertical projection of tree crowns (Korhonen et al., 2006). Canopy closure has a similar definition, but it expresses the proportion of the sky projected onto a plane (Paletto and Tosi, 2009).

2.3. Data analysis

To explore the relationship between macrofungal biodiversity (i.e., morphospecies richness and abundance) and potential explanatory variables, we performed generalized linear models (GLMs) using GenStat 12.0 (VSN International, Hemel Hempstead, UK). For the GLMs, we used a Poisson error structure and applied log-link function.

Two models were developed with (1) macrofungal morphospecies richness and (2) abundance as the response variables. Species richness models, in general, do not utilise information on the environmental requirements of individual species, even though each species has different environmental needs. To reduce the confounding effects associated with ignoring individual species requirements we developed separate GLMs for each macrofungal morphospecies functional groups. The macrofungal functional groups included ectomycorrhizal, wood-inhabiting, and terricolous saprotrophic fungi. Eight predictor variables were tested for both models: habitat type, air temperature, relative air humidity, soil pH, soil moisture, canopy cover, canopy closure, and substrate richness. Habitat type was fitted as a categorical predictor - logged peat swamp forest, large-scale oil palm plantation, monoculture versus polyculture smallholdings. We reported adjusted r-squared which corrects for the sample size and numbers of coefficients estimated. We conducted correlation tests for multi-collinearity (i.e., a state of very high inter-associations among variables) using global models that comprised all predictor variables (Supplementary Information). Since some explanatory variable pairs were characterized by strong collinearity ($|r| > 0.7$), predictor variables were dropped from the global model (Dormann et al., 2013).

To analyze the relationship between (dis)similarities in macrofungal community structure and (dis)similarities in environmental variables, the BIO-ENV method was performed. The Bray–Curtis fixed matrix based on the biotic data measured in the set of samples and the Euclidean-distance based matrices derived from all the possible sequential combinations of the abiotic variables. The BIO-ENV analysis allows the selection of the abiotic variable subset that maximizes the rank correlation between biotic and abiotic (dis)similarity matrices. Spearman rank coefficient was used to determine correlations between biological and abiotic parameters.

The similarity of substrate composition across the four habitats (logged peat swamp forest versus oil palm plantation areas) was evaluated using pairwise Bray-Curtis dissimilarities and visualized using non-metric multi-dimensional scaling (NMDS). The significance of substrate richness within habitats was investigated using one-way analysis of similarities (ANOSIM), a non-parametric multivariate analyses using PRIMER-E Ltd, Plymouth, UK (Clarke and Gorley, 2006). Analysis of similarity percentages (SIMPER) was also conducted to investigate the contribution of each substratum type to macrofungal occurrence within the studied habitats.

3. Results

3.1. General patterns of macrofungal biodiversity

In total, 757 clusters of macrofungi were collected (Supplementary Table 1). We recorded 61, 21, 21, and 24 morphospecies in logged peat swamp forest, large-scale plantation, monoculture smallholding and polyculture smallholding, respectively.

3.2. Drivers of macrofungal morphospecies richness

Table 1 and Fig. 2 present the results obtained from the analysis of macrofungal morphospecies richness. Macrofungal morphospecies richness was positively related to substrate richness. In contrast, macrofungal morphospecies richness was negatively related to soil pH and air temperature. Macrofungal morphospecies richness was also related to habitat type. Our results revealed that the peat swamp forest was associated with increase in macrofungal morphospecies richness (coefficient = 0.69) relative to the large-scale plantation. Similarly, both polyculture and monoculture smallholdings were associated with increase in macrofungal morphospecies richness (coefficient = 0.40 and coefficient = 0.32, respectively) relative to the large-scale plantation. This model explained 82.17% of the variation in macrofungal morphospecies richness. Only canopy closure had no significant effect on macrofungal morphospecies richness ($P > 0.05$).

3.3. Drivers of macrofungal abundance

We found that macrofungal abundance was positively related to substrate richness and relative air humidity (Table 1 and Fig. 3). In contrast, macrofungal abundance was negatively related to soil moisture and canopy closure. Macrofungal abundance was also influenced by habitat type. Among the habitats assessed in our study, the peat swamp forest was associated with increased macrofungal abundance (coefficient = 0.23) relative to the large-scale plantation. Likewise, the polyculture smallholding was associated with increased macrofungal abundance (coefficient = 0.10) relative to the large-scale plantation. Conversely, the monoculture smallholding was associated with decreased macrofungal abundance (coefficient = -0.27) relative to the large-scale plantation. The model explained 45.34% of the variation in macrofungal abundance.

Table 1

Generalized linear models (GLMs) evaluating the effect of environmental variables on macrofungal biodiversity on natural and modified peatlands.

Predictor variable	Coefficient	Wald statistic	P
Model 1 (morphospecies richness)			
Air temperature	−0.0381	10.90	<0.001
Soil pH	−0.2662	119.02	<0.001
Substrate richness	0.0905	58.79	<0.001
Habitat type:		81.77	<0.001
Peat swamp forest	0.6902		
Monoculture smallholding	0.3185		
Polyculture smallholding	0.3991		
Model 2 (total abundance)			
Relative air humidity	0.01649	5.76	0.016
Soil moisture	−0.1098	5.45	0.020
Canopy closure	−0.00719	4.19	0.041
Substrate richness	0.1872	37.09	<0.001
Habitat type:		9.83	0.020
Peat swamp forest	0.232		
Monoculture smallholding	−0.266		
Polyculture smallholding	0.093		
Model 3 (wood-inhabiting fungal abundance)			
Relative air humidity	0.02874	14.49	<0.001
Soil moisture	−0.1820	11.48	<0.001
Substrate richness	0.1943	28.24	<0.001
Habitat type:		8.66	0.034
Peat swamp forest	−0.282		
Monoculture smallholding	−0.334		
Polyculture smallholding	−0.040		
Model 4 (terricolous saprotrophic fungal abundance)			
Relative air humidity	−0.0674	8.372	<0.001
Substrate richness	0.2733	12.373	<0.001
Habitat type:		17.982	<0.001
Peat swamp forest	2.299		
Monoculture smallholding	0.149		
Polyculture smallholding	0.720		

3.4. Drivers of specific macrofungal functional group abundance

The abundance of wood-inhabiting fungi was positively related to substrate richness and relative air humidity, but it was negatively related to soil moisture (Table 1 and Fig. 4). In addition, the abundance of wood-inhabiting fungi was influenced by habitat type. Our results indicate that the peat swamp forest was associated with decreased wood-inhabiting fungal abundance (coefficient = −0.28) relative to the large-scale plantation. Monoculture and polyculture smallholdings were associated with decreased wood-inhabiting fungal abundance (coefficient = −0.33 and coefficient = −0.04, respectively) relative to the large-scale plantation. This model explained 22.54% of the variation in wood-inhabiting fungal abundance. Canopy closure had no significant effect on the abundance of wood-inhabiting fungi ($P > 0.05$).

Our results, as shown in Table 1 and Fig. 5, indicated that the abundance of terricolous saprotrophic fungi was positively related to substrate richness, but negatively related to relative air humidity. Habitat type had a significant effect on the abundance of terricolous saprotrophic fungi. Our results indicated that peat swamp forest was associated with increased terricolous saprotrophic fungal abundance (coefficient = 2.30) relative to the large-scale plantation. Monoculture and polyculture smallholdings were associated with increased terricolous saprotrophic fungal abundance (coefficient = 0.15 and coefficient = 0.72, respectively) relative to the large-scale plantation. This model explained 45.79% of the variation in terricolous saprotrophic fungal abundance. Both canopy closure and soil moisture had no significant effect on the abundance of terricolous saprotrophic fungi ($P > 0.05$).

Surprisingly, none of the predictor variables had a significant effect on the abundance of ectomycorrhizal fungi ($P > 0.05$). In summary, these results suggest that there is considerable variation in functional group responses to different environmental variables.

3.5. Relationships between macrofungal community structure and environmental variables

The BIO-ENV procedure was used to identify combinations of environmental variables that best associate the samples in a consistent approach with the macrofungal community structure (Table 2). The single variable that best matched macrofungal

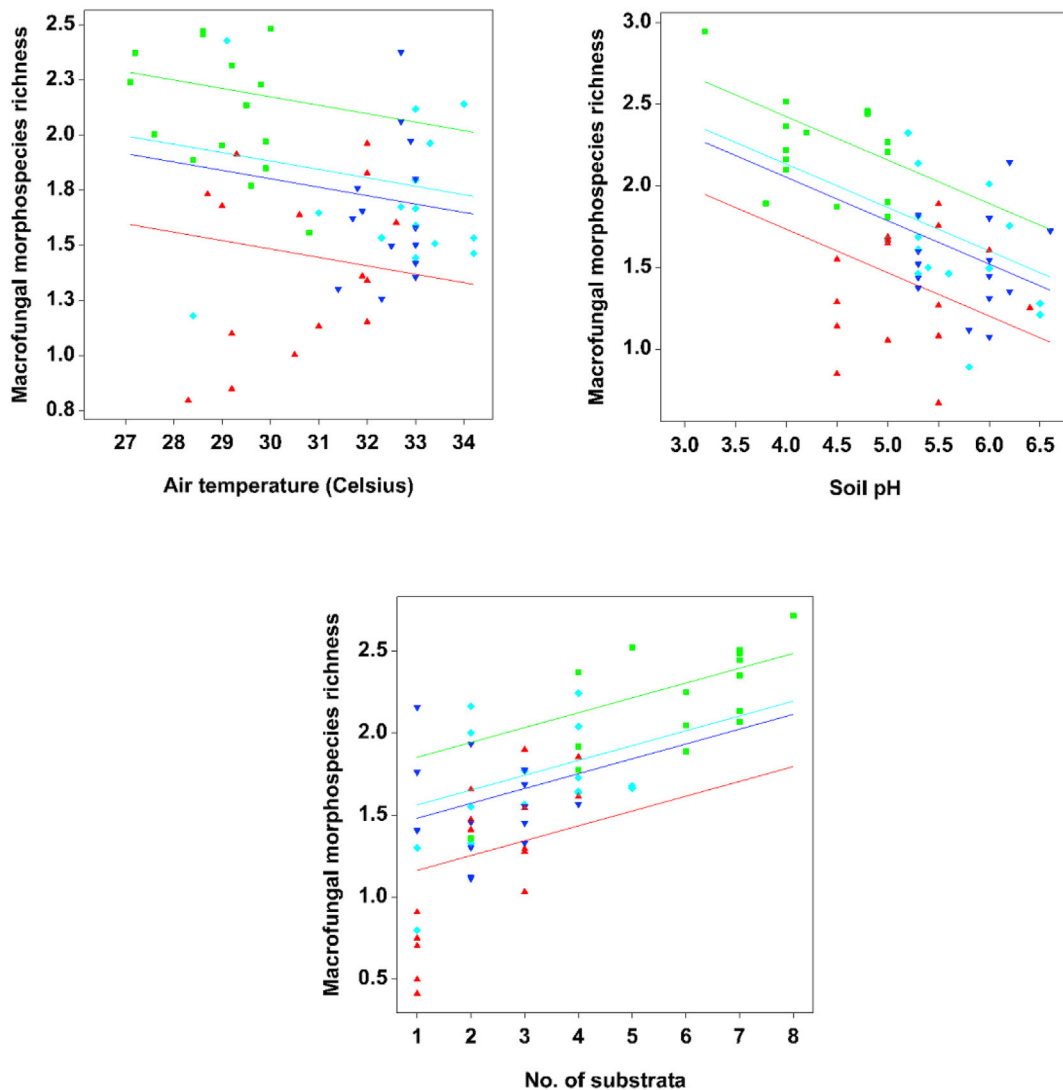


Fig. 2. Significant predictor variables for determining macrofungal morphospecies richness. Green represents peat swamp forest, dark blue represents large-scale plantation, light blue represents monoculture smallholding, and red represents polyculture smallholding. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

community structure was substrate richness, followed by canopy closure, air temperature, soil moisture, and relative air humidity. The combination of those environmental variables constituted the overall optimum ($\psi_s = 0.380$). Even though the BIO-ENV procedure does not provide the direction of correlations, it can indicate which variables affect differences in community structure between samples. The analysis showed that macrofungal communities among the studied areas seem to be influenced by substrate richness, microclimates, and soil characteristics.

3.6. Substrate composition

Substrate composition (richness) was significantly different between logged peat swamp forests and managed oil palm cultures (ANOSIM, $R_{\text{global}} = 0.586$; number of permutations: 999; $p < 0.001$) (Table 3). Fig. 6 depicts the compositional differences and similarities between sampled plots and shows a clear separation between peat swamp forest samples from oil palm plantation sample locations. According to the SIMPER analysis (Table 4), ten different substrata could be found in the logged peat swamp forests, where they made significant contributions to the total available resources for macrofungi. Here, macrofungi were predominantly found on coarse woody debris; on a substrate type, which was with marginal effects, or not available in the other studied habitat types. In the other three habitat types (on the different oil palm cultures), macrofungi were mostly found on oil palm fronds.

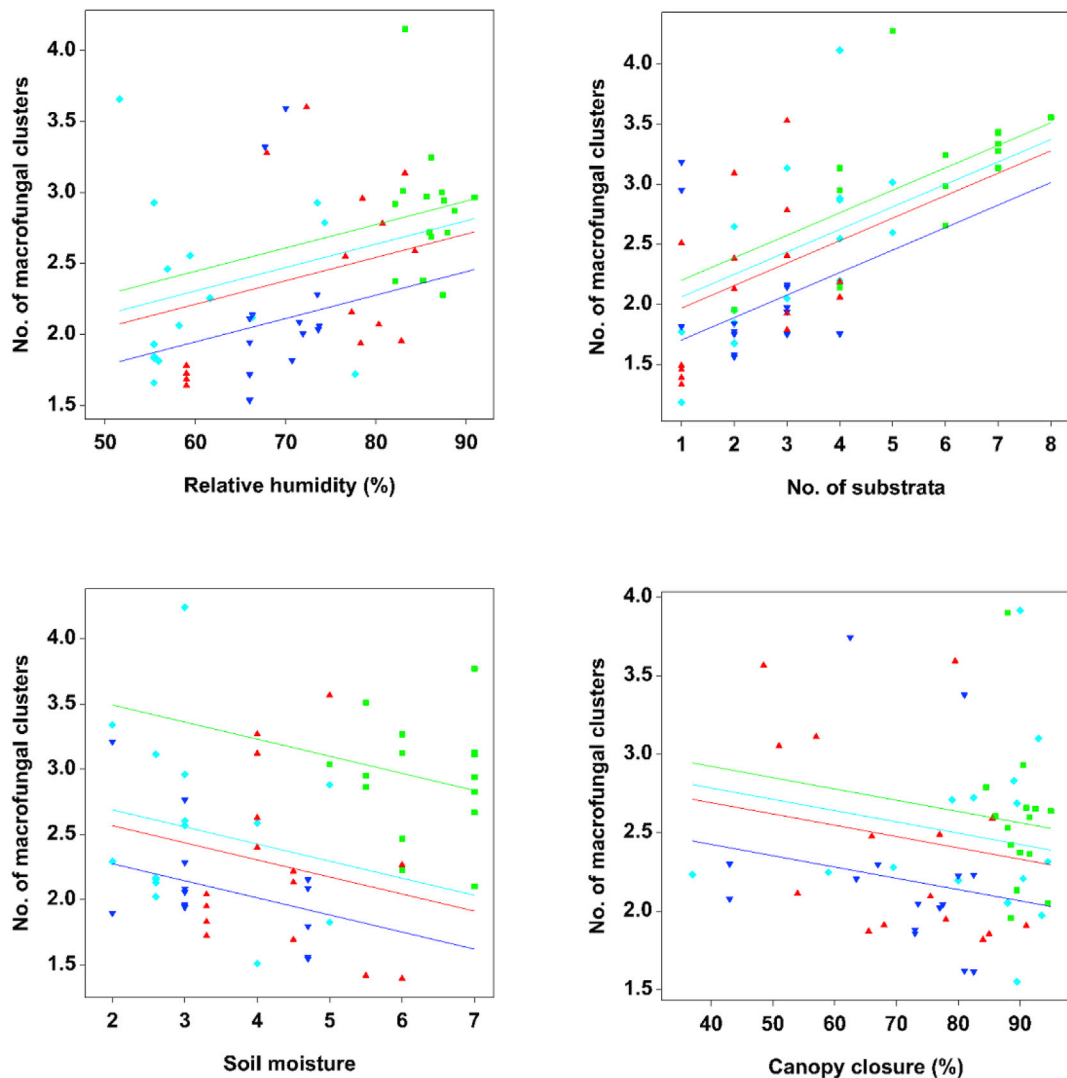


Fig. 3. Significant predictor variables for determining macrofungal abundance. Green represents peat swamp forest, dark blue represents large-scale plantation, light blue represents monoculture smallholding, and red represents polyculture smallholding. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

4. Discussion

4.1. Substrate composition under different peatland habitats

We found that macrofungal distribution patterns in different habitats were driven by various environmental variables including microclimatic variables, soil characteristics, and substrate properties. Peat swamp forest provided the most suitable microclimate and substrate richness and composition for macrofungi. Macrofungal morphospecies composition in logged peat swamp forests was found to be significantly different from those in oil palm plantations. Our findings indicate that forest conversion to large- or small-scaled oil palm monoculture system has greater negative impacts on macrofungal diversity than conversion to oil palm polyculture system. Compared to monoculture smallholdings, polyculture smallholdings seem to provide slightly more suitable habitat for macrofungi since they provided more and larger volumes of dead plant materials (e.g., coarse woody debris). By contrast, large-scale oil palm plantations harboured a lower number of substrata often with less woody available plant materials and with lower abundance of plant remnants compared to the habitats can be found in smallholdings.

In addition, large- or small-scaled, homogeneous (e.g., equal stand age) areas of oil palm monocultures are particularly likely to be unfavourable for in-situ biodiversity conservation (Azhar et al., 2015). The use of agrochemicals (e.g., fertilizers and pesticides) is common in monoculture plantations to control weeds, pest, and fungus (Azhar et al., 2015). For example,

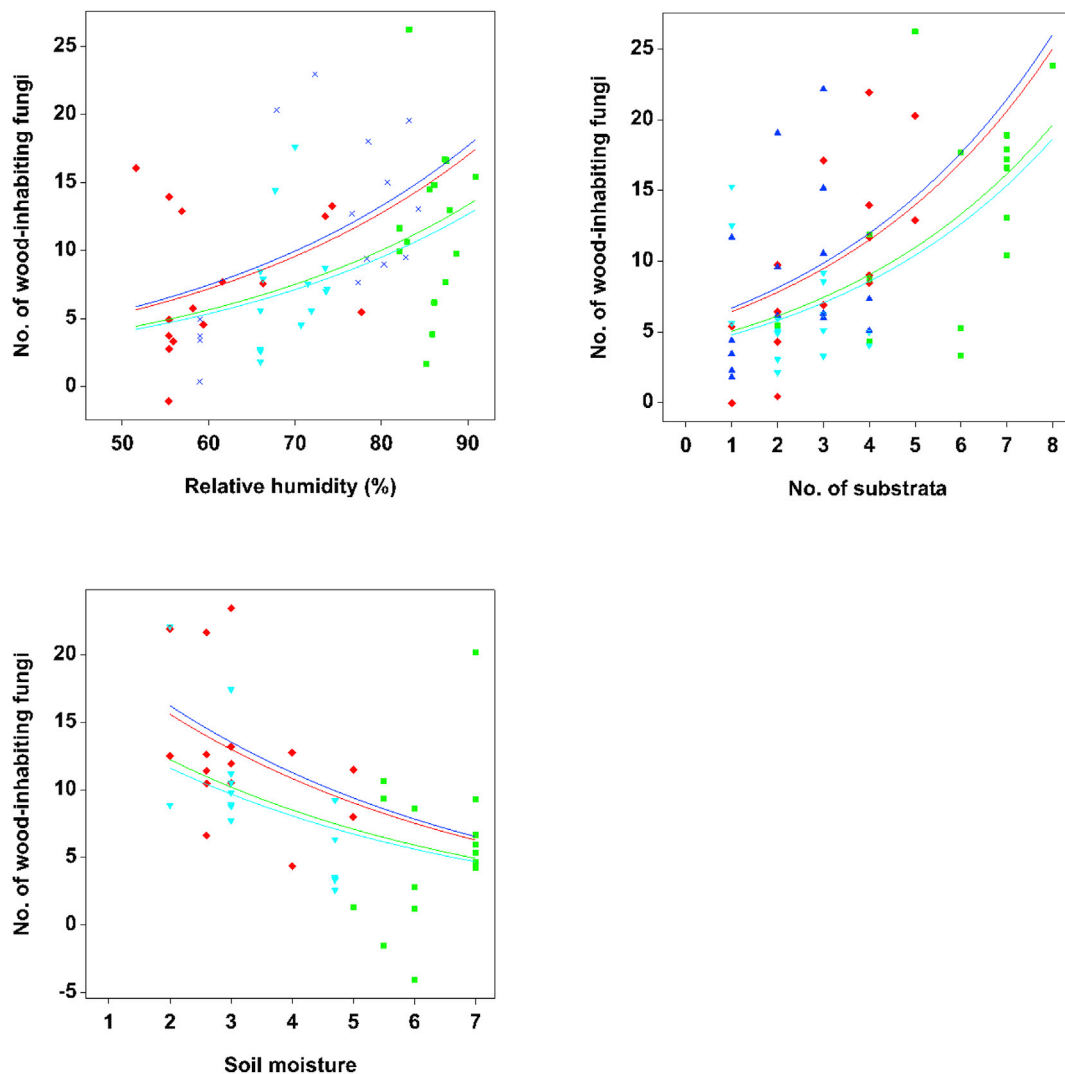


Fig. 4. Significant predictor variables for determining the abundance of wood-inhabiting fungi. Green represents peat swamp forest, dark blue represents large-scale plantation, light blue represents monoculture smallholding, and red represents polyculture smallholding. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

the fungicide hexaconazole is used to control the white rot fungus, *Ganoderma*, which causes decay in oil palm (Maznah et al., 2017) and may have detrimental effects on macrofungal biodiversity.

4.2. Factors influencing macrofungal morphospecies richness

Land use change affects biodiversity and ecological processes through changes in the local climate and modification of habitats (Hardwick et al., 2015; Anamulai et al., 2019). In the tropics, deforestation can cause a change in the local climate resulting in rising temperatures and increasing water stress (Voldoire and Royer, 2004; Mitchard, 2018). Temperature is one of the most vital determinants driving macrofungal growth (Tuomela et al., 2000). Our results suggest that macrofungal morphospecies richness declined with increasing temperatures, which are consistent with Brown et al. (2006) who reported that cultivation areas were unable to support forest macrofungi due to the increased temperature.

As it was expected, logged peat swamp forests supported greater macrofungal species richness compared to large-scale oil palm plantation, monoculture, and polyculture smallholdings. Logged peat swamp forests have greater habitat heterogeneity compared to all oil palm habitats, and therefore, provide a greater diversity of substrata and more suitable environmental conditions for macrofungal growth. A greater macrofungal diversity was also found in the more humid forest landscapes; the three different oil palm plantations harboured, however, less diverse but unique assemblages of macrofungi. This is consistent with Li et al. (2018b) who showed that native forests had a higher diversity of macrofungi than plantation forests.

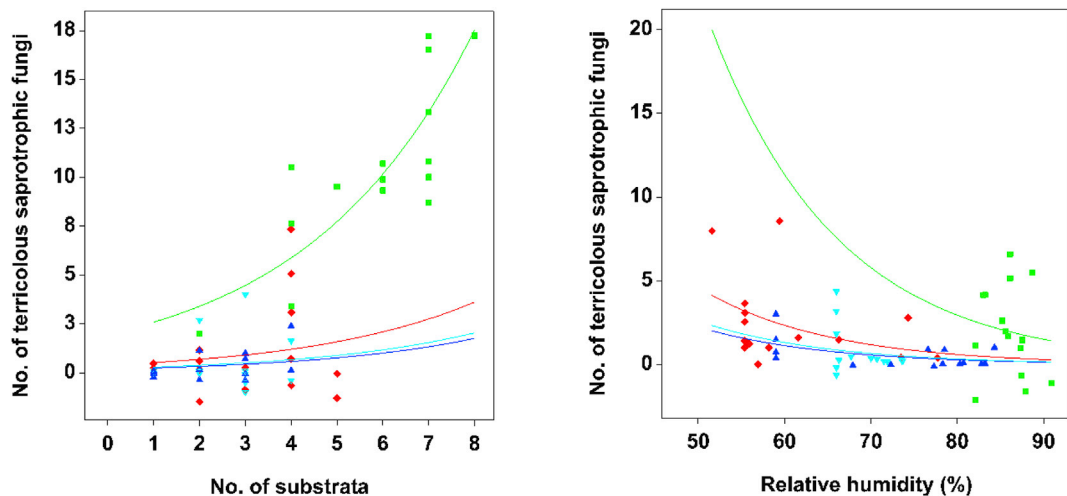


Fig. 5. Significant predictor variables for determining the abundance of terricolous saprotrophic fungi. Green represents peat swamp forest, dark blue represents large-scale plantation, light blue represents monoculture smallholdings, and red represents polyculture smallholdings. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

Table 2

BIO-ENV analysis of the relationship between the macrofungal community structure and environmental variables. Overall optimum is indicated in bold.

k	Spearman rank coefficient	Best variable combinations
1	0.223	Substrate richness
2	0.278	Canopy closure, substrate richness
3	0.328	Canopy closure, substrate richness, air temperature
4	0.362	Canopy closure, substrate richness, air temperature, soil moisture
5	0.380	Canopy closure, relative air humidity, substrate richness, air temperature, soil moisture
6	0.349	Canopy closure, relative air humidity, substrate richness, air temperature, soil moisture, canopy cover
7	0.325	Canopy closure, relative air humidity, substrate richness, air temperature, soil moisture, soil pH, canopy cover

Table 3

Analysis of similarities (ANOSIM) based on substrate composition of logged peat swamp forest (PSF), large-scale oil palm plantation (OPE), monoculture smallholding (MS) and polyculture smallholding (PS).

Comparisons	R-value	P
PSF, OPE	0.993	0.001
PSF, MS	0.984	0.001
PSF, PS	0.815	0.001
OPE, MS	0.079	0.068
OPE, PS	0.28	0.001
MS, PS	0.253	0.001

n = 15.

The conversion of tropical forests into oil palm plantations has been shown to affect soil properties including soil pH (Ismawi and Ahmed, 2012). We found that macrofungal morphospecies richness was significantly dependent on soil pH. The high coefficient values for soil pH in our models suggest that many macrofungal species in the peat swamp forests prefer for acidic soil conditions. The acidic soil conditions found in peat swamps would provide unique habitat (in terms of the vegetation community and therefore substrata and soil conditions) and thus host a unique range of macrofungi unlikely to be found elsewhere, adding to the conservation value of these habitats.

High substrate diversity is an important driver of macrofungal distribution and growth (Ye et al., 2019). Our results showed a positive relationship between macrofungal morphospecies richness and substrate richness. This result is in agreement with the results of Hattori et al. (2012) and Yamashita et al. (2015) on polypore fungi found in forests and cultivation areas in the tropical regions. They reported that forest conversion to crop plant plantations reduced substratum availability significantly.

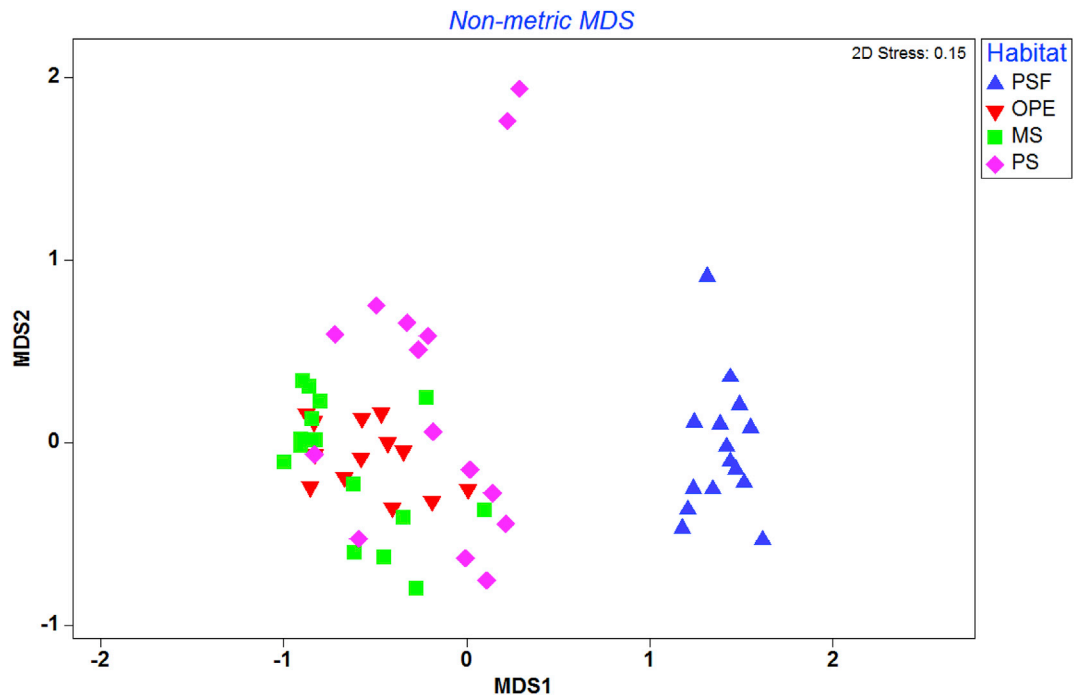


Fig. 6. Non-metric Multidimensional Scaling (NMDS) plot showing the compositional differences of substrata between habitats: PSF = peat swamp forests, OPE = large-scale oil palm plantations, MS = monoculture smallholdings, PS = polyculture smallholdings.

Table 4

Composition of substrata analysed with SIMPER based on the contribution (%) of each environmental driver (type of substrate) to the dissimilarity among fungal species groups derived from a Bray-Curtis dissimilarity matrix built on fungal species abundances.

Habitat	Type of substrate	Contribution (%)	Cumulative contribution (%)
Peat swamp forest	Coarse wood	32.87	32.87
	Soil	12.83	45.70
	Leaf litter	12.36	58.06
	Twig	10.53	68.58
	Fallen tree	9.62	78.21
	Living tree	9.40	87.61
	Stump	6.51	94.11
	Branch	4.81	98.92
	Trunk	0.82	99.75
Large-scale plantation	Fruit shell	0.25	100.00
	Oil palm frond	91.94	91.94
	Trunk	4.90	96.85
	Coarse wood	1.19	98.04
	Soil	1.15	99.19
	Stump	0.81	100.00
Monoculture smallholding	Oil palm frond	82.19	82.19
	Living oil palm	9.18	91.37
	Soil	4.39	95.76
	Trunk	2.48	98.24
	Buttress	1.34	99.58
	Coarse wood	0.42	100.00
Polyculture smallholding	Oil palm frond	51.40	51.40
	Fallen coconut tree	15.12	66.52
	Coarse wood	13.61	80.14
	Trunk	12.84	92.98
	Buttress	5.47	98.45
	Stump	1.16	99.61
	Soil	0.39	100.00

4.3. Factors influencing macrofungal abundance

Macrofungal abundance was driven by substrate richness, relative air humidity, soil moisture, canopy closure, and habitat type. The most important driver was substrate richness as it increased with the number of observed macrofungal clusters. Plant/wood-based substrata are important habitats and substratum resources for macrofungi (Boddy, 2001; Baber et al., 2016; Kahl et al., 2017).

Macrofungal abundance was also influenced by environmental conditions. High relative air humidity had positive effects on macrofungal abundance. According to Jang and Hur (2014), fungi favour air humidity higher than 82%. While, macrofungal abundance was negatively associated with canopy closure. In areas with closed canopies created by the dense foliage of trees and shrubs, temperature and moisture conditions become less favourable for decomposition (Dighton and Mason, 1985). Great tree canopy cover reduces light, rainfall, temperature and moisture, and hence slows down decomposition. Senn-Irlet and Bieri (1999) found a similar pattern with sporocarp abundance doubling in younger open stands, although species richness increased in mature closed-canopy forest. Canopy cover was, however, found to be less significant for saprotrophic fungi compared to the availability of specific substrata (Lodge et al., 1995; Santos-Silva et al., 2011). Tree canopy is an important factor affecting the dynamics of forest ecosystems and habitat formation (Nakamura et al., 2017). Trees can promote or suppress the growth and distribution of understory species, including macrofungi under changing light conditions (Barbier et al., 2008; Thomaes et al., 2013).

Soil moisture was found to have negative effects on macrofungal. Similar findings were reported by Bowens (2009), indicating that basidiomycetes are intolerant to the anaerobic soil conditions of waterlogged stands. Even though low precipitation limits the fruiting of macrofungi, excess moisture can also inhibit fruiting in some species (Lodge et al., 2004).

4.4. Factors influencing macrofungal functional groups

The abundance of wood-inhabiting fungi was driven primarily by substrate richness, while relative air humidity, soil moisture, and habitat type play minor roles. Within our study sites higher logging residues including woody debris from tree felling (e.g., branches, leaves, stumps, roots, tops, bark) and pruned oil palm fronds in large-scale oil palm plantation (Germer and Sauerborn, 2008; Hattori et al., 2012; Juutilainen et al., 2017) contributed to increased substrate richness. Pruned oil palm fronds are left to naturally decay in the large-scale plantation with this process dominated by *Schizophyllum commune*, the most dominant wood-inhabiting species (84.3%) in large-scale plantations. Dead wood size (Heilmann-Clausen and Christensen, 2004; Lonsdale et al., 2008) and decay stage (Heilmann-Clausen and Christensen, 2003; Mäkipää et al., 2017) also contribute to the abundance of wood-inhabiting fungi in the large-scale plantation.

Logged peat swamp forests had the highest abundance for terricolous saprotrophic fungi, most likely because of the amount of forest litter. Talbot et al. (2013) reported that litter quantity is one of the most important factors influencing terricolous fungi. Terricolous saprotrophic fungi such as *Inocybe* sp. (25.11%) and *Marasmius* sp. (23.91%) dominated the peat swamp forest, mainly found on forest litter. Tree species composition, which is higher in logged peat swamp forests, also contributed to the high abundance terricolous saprotrophic fungi (Kutszegi et al., 2015).

4.5. Linking the macrofungal community structure to changes of the environmental variables

We found that the macrofungal community structure was mainly driven by substrate richness, followed by canopy closure, air temperature, soil moisture, and relative air humidity. Similarly, Packham et al. (2002) found that variation in the macrofungal communities was correlated with a different set of the measured environmental variables in mature and young regrowth Tasmanian wet forests. In contrast, Chen et al. (2018) suggest that spatial processes (e.g., dispersal limitation) and light availability were the most important factors affecting the macrofungal community in the temperate deciduous broad-leaved forest.

4.6. Substrate composition under different peatland habitats

Our study showed that logged peat swamp forests were characterized by diverse substrate composition compared to large-scale oil palm plantation, monoculture, and polyculture smallholdings. Coarse woody debris and twigs are some of the most frequently observed substrata preferred by macrofungi in natural forests (Yamashita et al., 2015). Santos-Silva et al. (2011) also reported similar results when studying the distribution of saprotrophic fungi; a strong correlation between the amount of coarse or fine woody debris and the diversity of saprotrophic fungi. Our study also suggests that substrate diversity is important in determining the abundance of saprotrophic fungi in forests.

We found that there was no significant difference in substrate composition between large-scale oil palm plantation and monoculture smallholdings. According to the SIMPER analysis, our results show that most substrata available in oil palm habitats were oil palm fronds. Oil palm fronds are regularly cut during pruning and harvesting of fresh fruit bunches. Pruned fronds are usually stacked on top of dense ground vegetation at the thickness of 30–40 cm (Tao et al., 2016). Seven types of substrata were identified in polyculture smallholdings, greater than large-scale plantations and monoculture smallholdings. The amount of biomass generated is likely to be greater in polyculture smallholdings, compared to large-scale plantations and monoculture smallholdings.

4.7. Limitations of data

There were a number of limitations associated with conducting research in tropical peninsula Malaysia. We sampled fungal genera (mixed with species) rather than well-identified species. Most fungal species have not currently been described in Malaysia, and are new to science. Hence, we had to stop identification at the genus level. Most biodiversity oriented studies, including our study, generally rely on fruiting bodies for identification as it is difficult to identify fungi based on mycelia, which are usually cryptic and morphologically indistinctive (Ovaskainen et al., 2013). Our survey may result in several overlooked sporocarps of certain fungal species because a limited time period was spent on finding sporocarps at the plots. Therefore, the current results should be viewed with caution.

5. Conclusion

This study highlights the importance of logged peat swamp forest in supporting macrofungal biodiversity. Each habitat had distinct macrofungal communities, however, not even heterogeneous polyculture smallholdings can be a substitute for peat swamp forest in terms of supporting macrofungal diversity. Nevertheless, polyculture smallholdings should not be discounted and further research is needed to assess their contribution to biodiversity, especially in places where plant species composition is different from our region. The ability of polyculture smallholdings to decrease the negative effects of deforestation should be measured in future studies. Further deforestation of natural peatlands or conversion to industrial oil palm agriculture will greatly reduce tropical macrofungal morphospecies richness and functional ecology. The expansion of oil palm plantations will be to the detriment of peat swamp forests and should not be allowed in the future to conserve fungal biodiversity. Substrate composition in logged peat swamp forests should be replicated artificially in oil palm plantations to promote and permanently maintain macrofungal biodiversity in managed habitats. Forest conversion and rising temperature with changing climatic conditions will also be strong drivers of macrofungal biodiversity loss in the future.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.gecco.2020.e01122>.

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